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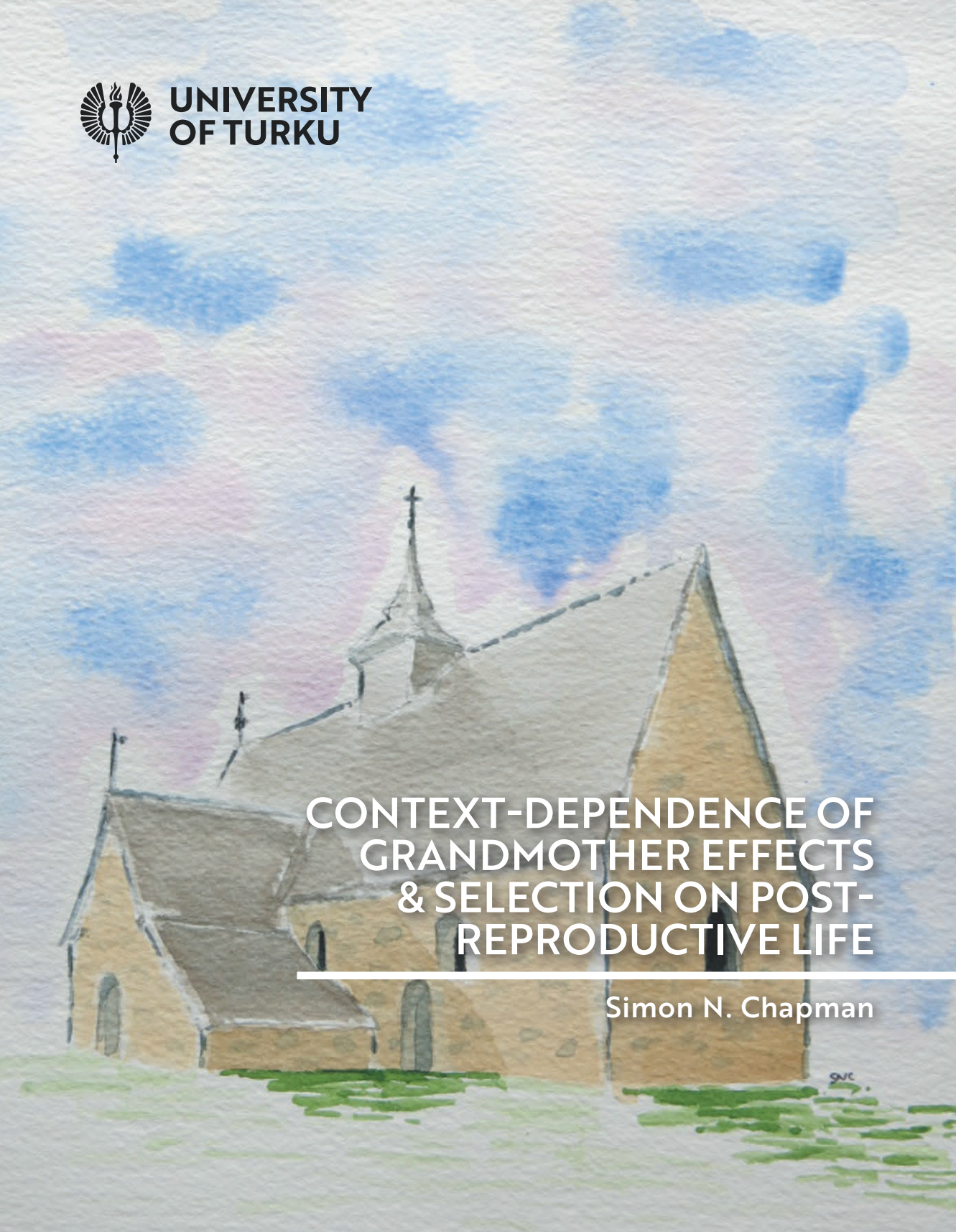

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“We like pulling the heads off sheep”
“…and teacakes”
- *Monty Python’s ‘Hell’s Grannies’*

ABSTRACT

In cooperatively breeding species, the amount of help provided and the outcomes of that help can vary greatly under different contexts, such as helper age, sex of the offspring, or age of the offspring. Contextual variation in the outcomes of help has been less well studied from an evolutionary perspective in humans. As the indirect fitness gains from grandmothering have been hypothesised to have contributed to the evolution of prolonged post-reproductive life, we now need to understand the contexts under which grandmothering is or is not beneficial. Without knowledge of whether there is contextual-dependence in the outcomes of grandmother presence, we cannot hope to understand the role of grandmothering in the evolution of extended post-reproductive life.

Using an extensive genealogical dataset from pre-industrial Finland with natural fertility and mortality rates, I investigate how survival and fertility outcomes of grandmother presence may differ under different contexts and discuss how this may affect selection on lifespan. I first quantify the demographics of grandmotherhood, providing information on the opportunity and need for help. I then focus on five main contexts: i) age of grandchildren, ii) lineage of grandmother (paternal or maternal), iii) sex of grandchildren, iv) adverse birth status (e.g. born as a twin), and v) grandmother age.

I found that before the demographic transition to lower fertility and childhood mortality, the opportunity for grandmothers to help (i.e. presence) was relatively stable. Post-transition, grandmothers were alive for more of their grandchildren's lives, but an increasing percentage of grandmothers lived in other parishes, changing the opportunity to help and the dynamics of the grandmother-grandchild relationship. I found that grandmother presence was only beneficial for grandchildren of a certain age (2-5 years old), and then only if the maternal grandmother was present. Maternal grandmother presence also reduced the time between births but did not have any effect on age at first birth. There was a slight sex bias in outcomes of grandmother help, but not enough to have driven the differences between maternal and paternal lineages. Surprisingly, grandmothers did not mitigate most of the adverse birth statuses, only improving survival outcomes for those born preceding a short (<24 months) birth interval. I also found that grandmother age was important, with younger maternal grandmothers beneficial to grandchild survival whereas older and weaker paternal grandmothers were detrimental to the survival of their infant grandchildren.

In identifying and investigating different contexts of grandmothering, I have shown that beneficial outcomes of grandmother presence are not guaranteed, and, in some contexts, grandmothers may even have adverse effects. My novel findings suggest that any selection for extended post-reproductive lifespan from grandmothering will, therefore, be somewhat weaker than previously considered, at least in agricultural populations such as this. Future work should further investigate the context-dependence of grandmothering to help clarify the magnitude of grandmothering's role in the evolution of post-reproductive lifespan.

KEYWORDS: context-dependence, cooperative breeding, fertility, grandmother hypothesis, inclusive fitness, mortality

TIIVISTELMÄ

Yhteisöllisesti elävien eläinten toisille yksilöille tarjoaman avun määrä ja kelpoisuusvaikutukset voivat vaihdella suuresti eri olosuhteissa, kuten sekä auttajan että avun saajan iän ja sukupuolen mukaan. Erilaisten olosuhteiden vaikutusta auttamisen seurauksiin on tutkittu ihmisillä vähän evolutiivisesta näkökulmasta. Koska evolutiivisen hypoteesin mukaan isoäitien avun tuoma epäsuora kelpoisuus on vaikuttanut pitkän menopaussin jälkeisen eliniän evoluutioon ihmisillä, tulee ymmärtää, millaisissa tilanteissa tai olosuhteissa isoäidin apu on tai ei ole hyödyllistä kelpoisuuden kannalta. Ilman tietoa olosuhteiden vaikutuksesta isoäitivaikutusten voimakkuuteen on mahdotonta ymmärtää isoäitiyden roolia pitkän menopaussin jälkeisen eliniän selittäjänä.

Historiallisista suomalaisista kirkonkirjoista kerätyn kattavan aineiston avulla tutkin, kuinka isoäidin läheisyys vaikutti sekä lastenlasten elossasäilymiseen, että aikuisten lastensa hedelmällisyyteen erilaisissa olosuhteissa, ja pohdin näiden vaikutusten yhteyttä pitkän eliniän evoluutioon. Ensimmäiseksi tarkastelen isoäitiyden demografiaa ja selvitän miten paljon isoäideillä oli tilaisuuksia auttaa jälkeläisiään esiteollisena aikana Suomessa, eli miten pitkään isoäiti oli elossa lastenlasten syntymän jälkeen ja asuiko hän lastenlastensa lähettyvillä. Tämän jälkeen tarkastelen isoäitivaikutuksia viidessä eri kontekstissa: i) lapsenlapsen iän, ii) isoäidin sukulinjan (oliko sukulaisuus isän- tai äidinpuoleista), iii) lapsenlapsen sukupuolen, iv) tai muun epäsuotuisan syntymähetken olosuhteen (esim. kaksosuus), ja v) isoäidin iän suhteen

Esiteollisena aikana ja ennen väestöllistä muuntumista kohti alhaista syntyvyyttä ja kuolleisuutta isoäitien ja lastenlasten yhteinen jaettu elinaika ja näin ollen isoäitien mahdollisuus auttaa pysyi melko muuttumattomana. Myöhemmin, väestöllisen muuntumisen jälkeisenä aikana isoäidit olivat elossa pidempään lastenlastensa elämässä, mutta enenevissä määrin he kuitenkin asuivat eri kunnissa kuin lapsenlapsensa, mikä vaikutti isoäitien mahdollisuuksiin auttaa. Tutkimukseni paljasti, että isoäidit vaikuttivat positiivisesti lastenlastensa elossasäilyvyyteen lastenlasten ollessa 2-5 vuoden ikäisiä, ja vain äidinpuolen isoäitien vaikutus oli positiivinen. Äidinpuolen isoäitien läsnäolo lyhensi myös aikuisten tyttärien synnytysvälejä, mutta ei kuitenkaan vaikuttanut ensimmäisen lapsen saanti-ikään. Tytöt ja pojat hyötyivät hieman eri tavoin isoäitien läsnäolosta, mutta tämä ero ei ollut riittävä selittämään äidinäidin ja isänäidin vaikutusten eroa. Yllättäen, isoäitien läsnäolo ei auttanut useimmissa tutkituissa epäsuotuisissa syntymäolosuhteissa; isoäiti paransi ainoastaan niiden lasten elossasäilyvyyttä, jotka saivat pikkusisaruksen alle 2-vuotiaina. Isoäidin oma ikä oli tärkeä, sillä vaikka nuoremmat äidinäidit paransivat lastenlastensa elossasäilyvyyttä, vanhat yli 75-vuotiaat, ja heikommassa kunnossa olevat isänäidit lisäsivät imeväisikäisten lastenlastensa kuolleisuutta.

Tutkimalla isoäitien vaikutuksia eri olosuhteissa, voin todeta, että positiiviset isoäitivaikutukset eivät ole aina havaittavissa ja jossain olosuhteissa isoäideillä voi olla jopa haitallisia vaikutuksia. Tutkimustulokseni osoittavat, että luonnonvalinnan vaikutus menopaussin jälkeiseen elinikään isoäitivaikutusten kautta saattaa olla heikompaa kuin aikaisemmissa tutkimuksissa on arvioitu, ainakin tutkimuspopulaation kaltaisissa maatalousyhteisöissä. Tulevissa tutkimuksissa tulisikin huomioida isoäitivaikutusten riippuvuus erilaisista olosuhteista ja selvittää isoäitivaikutusten voimakkuus/suuruus pitkän menopaussin jälkeisen eliniän evoluution selittäjänä.

ASIASANAT: olosuhteet, yhteisöllinen lisääntyminen, hedelmällisyys, isoäitihypoteesi, kokonaiskelpoisuus, kuolleisuus

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Abbreviations

AIC	Akaike Information Criterion
GLMM	Generalised Linear Mixed-Effects Model
MGM	Maternal Grandmother
OR	Odds Ratio
PGM	Paternal Grandmother
PRLS	Post-Reproductive Lifespan
PrR	Post-Reproductive Representation
PrT	Post-Reproductive Time

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I Chapman SN, Pettay JE, Lahdenperä M & Lummaa V. Grandmotherhood across the demographic transition. *PLoS ONE*, 2018; 13(7): e0200963.

II Chapman SN, Lahdenperä M, Pettay JE, Lynch RF & Lummaa V. Offspring fertility and grandchild survival enhanced by maternal grandmothers in a pre-industrial human society. *Manuscript*

III Chapman SN, Pettay JE, Lummaa V & Lahdenperä M. Limited support for the X-linked grandmother hypothesis in pre-industrial Finland. *Biology Letters*, 2018; 14: 20170651.

IV Nenko I, Chapman SN, Lahdenperä M, Pettay JE & Lummaa V. Will granny save me? Birth status, survival, and the role of grandmothers. *Manuscript*

V Chapman SN, Pettay JE, Lummaa V & Lahdenperä M. Limits to fitness benefits of prolonged post-reproductive lifespan in women. *Current Biology*, 2019; 29(4): 645-650.

Data and code used in this dissertation are available as supplementary files alongside the online versions of record. Other supplementary information can be found after the last original publication.

Author contributions to original publications can be found in each chapter.

1 Introduction

Cooperative breeding systems are those in which non-parent individuals aid in the rearing of young, and can be found in birds, mammals, fish, and insects. It is, however, relatively rare as a breeding system, with 3-9% of birds (depending on definition) (Arnold & Owens 1998; Cockburn 2006) and less than 1% of mammals (Lukas & Clutton-Brock 2017) classed as cooperative breeders. Many cooperatively breeding species live in poor or variable environments (Rubenstein & Lovette 2007; Jetz & Rubenstein 2011; Lukas & Clutton-Brock 2017; Guindre-Parker & Rubenstein 2018), and helpers are typically non-reproductive, either because they are physiologically incapable of reproduction e.g. eusocial insects (Wilson 1971), because reproductive opportunities are lacking in their current environment e.g. Siberian jays *Perisoreus infaustus* (Ekman & Griesser 2002), because they are subordinate e.g. meerkats *Suricata suricatta* (Clutton-Brock et al. 1998), or because they failed to breed successfully in that year e.g. long-tailed tits *Aegithalos caudatus* (Glen & Perrins 1988; Hatchwell et al. 2001). Staying and helping can, therefore, be at least somewhat beneficial when there is little to no possibility of gaining immediate direct fitness.

In these breeding systems, though help can be directed to non-related individuals (Riehl 2013), help is typically kin-directed (Hatchwell 2009). Humans are cooperative breeders too (Mace & Sear 2005; Isler & van Schaik, 2012), and cooperation amongst our ancestors likely led to the evolution of the life-history traits that distinguish humans from other primates, such as large brain size (Isler and van Schaik 2012), short interbirth intervals (Hawkes et al. 1998; Mace & Sear 2005) longer developmental (juvenile) period (Hawkes et al. 1998; Isler & van Schaik, 2012), and, central to this thesis, extended post-reproductive life (Hawkes et al. 1998).

The evolution of extended post-reproductive lifespan (PRLS) - that is, prolonged life after reproduction has ceased - is a long-standing puzzle in evolutionary biology (Croft et al. 2015). Traditional life history theory operates under the assumption that reproduction and lifespan will end at the same time, thus maximising biological fitness (Stearns 1992; Roff 2002), yet individuals in a post-reproductive state can no longer gain fitness from their own reproduction i.e. no direct fitness. Humans are

part of a select group of animals that defy this assumption of life history theory and are characterised by an extended post-reproductive female life. Mechanistically, reproductive cessation (menopause) in humans occurs due to loss of ovarian follicular activity. Indirect fitness benefits of helping offspring fertility and grandoffspring survival have been hypothesised as one of the major drivers of the evolution of such human PRLS – the 'grandmother hypothesis' (Hawkes et al. 1998).

Contextual expression of human cooperative behaviours, however, are understudied and underappreciated from a theoretical standpoint. The evolutionary significance of a helping benefit of grandmothers could differ greatly if grandmother presence is beneficial only in specific circumstances or even becomes detrimental under certain conditions (e.g. Borgerhoff Mulder 2007; Strassmann and Garrard 2011). In the cooperative breeding animal literature, context-dependent helping has great importance – when and who helps, and the outcomes of that help are central in furthering understanding of the different pathways to this relatively rare breeding system. Propensity to help and outcomes of help can differ greatly under different contexts, such as age of the helper, age of the offspring, resource availability – both with positive and negative outcomes – sex, and relatedness of helpers to offspring (Hamilton 1964; Komdeur 1994; Legge 2000; Clutton-Brock et al. 2001; Clutton-Brock et al. 2002; Allainé & Theuriau 2004; Baglione et al. 2006; Ridley & Raihani 2007; Canestrati et al. 2008; Bruintjes et al. 2010; Koenig & Walters 2011; Nichols et al. 2012; Klauke et al. 2014; Zöttl et al. 2016).

In this thesis, I take a close look at the life history outcomes of grandmothering through the lens of context-dependence. In other words, when is the presence of grandmothers useful, and when is it not? Before we arrive at the specific aims of this thesis, we must first review what post-reproductive lifespan is and why it remains such a puzzle.

1.1 Post-reproductive life

The idea of PRLS being a unique and defining trait of *Homo sapiens* amongst primates (e.g. Pavelka & Fedigan 1991; Hawkes et al. 1998) has been misinterpreted as a claim of post-reproductive life being a unique trait of humans amongst all animals, and therefore considered as another case of human exceptionalism (e.g. Cohen 2004). There are those who view post-reproductive life as a general trait of mammals (Cohen 2004; Finch & Holmes 2010; Nichols et al. 2016), arguing that humans are one among many. They are not wrong: the proportion of life spent post-reproductively is mathematically constrained to be above zero. However, those positing that PRLS is a life history trait that separates humans from other primates are not claiming that no other mammals demonstrate post-reproductive life, but that it is an extended post-reproductive lifespan that is so unusual. To evolve, it requires

a decoupling of somatic and reproductive senescence (Cohen 2004) far beyond that which could arise from individual variation in senescence rates.

One recent approach for statistically calculating whether a species has extended post-reproductive life or not is post-reproductive representation (PrR), which uses age-specific rates of fecundity and survival, and accounts for all individuals, whether they died before the average age of reproductive cessation or not (Levitis & Lackey 2011, Levitis et al. 2013). Ellis and colleagues (2018a) calculated PrR for 52 species of wild mammal (using both cross-sectional and longitudinal data), and showed that many mammals reported to have post-reproductive life do not have an extended post-reproductive life. A further two species of whale were shown to be menopausal on the basis of ovarian scarring, which occurs in some species following ovulation (Ellis et al. 2018b). PrR, though not infallible (Chapman et al. 2019), is statistically valid (Levitis & Lackey 2011) and is currently the best tool available for determining the presence of extended post-reproductive lifespan at the species-level.

With the PrR approach, we are therefore left with a short list of menopausal species with extended post-reproductive life: humans, short-finned pilot whales (*Globicephala macrorhyncus*), killer whales (*Orcinus orca*), beluga whales (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*) (Ward et al. 2009; Foster et al. 2012; Ellis et al. 2018a; Ellis et al. 2018b). False killer whales (*Pseudorca crassidens*) may be the fifth non-human menopausal mammal species (Photopoulou et al. 2017), but results from ovarian analyses are mixed, and more data is needed (Photopoulou et al. 2017; Ellis et al. 2018b). Asian elephants (*Elephas maximus*) also demonstrate significant post-reproductive periods (Lahdenperä et al. 2014; Chapman et al. 2019), but this is likely reproductive cessation due to age-specific changes in behaviour or body condition, rather than due to physiological incapability (Chapman et al. 2019). There are also reported cases of post-reproductive females in other species (Packer et al. 1998; Pavelka et al. 2002; Uematsu et al. 2010), but these are almost certainly statistical artefacts (Levitis & Lackey 2011; Ellis et al 2018a) or a consequence of behavioural decisions, rather than true physiological reproductive cessation and prolonged life thereafter.

The take-home message thus far is that the major evolutionary puzzle is not the existence of post-reproductive life per se, but the development of extended post-reproductive life. This is by no means a recent question (see e.g. Williams 1957), though much of our current understanding comes from work in the last few decades. In the next section, I will briefly review the main adaptive hypotheses that are still considered as plausible drivers of extended PRLS.

1.2 Adaptive hypotheses for PRLS

Whilst this section is primarily concerned with adaptive hypotheses, there are also a number of non-adaptive hypotheses proposed (see Croft et al. 2015), a couple of which are noteworthy: i) PRLS in modern humans is due to medicine and good environment allowing life to continue after menopause; and ii) selection operates on male lifespan, and that female lifespan is a by-product of that (Marlowe 2000; Tuljapurkar et al. 2007). They do not, however, withstand closer scrutiny: i) the evidence for PRLS in contemporary and historic human populations without access to modern medicine is strong (Levitis et al. 2013), and though expected lifespan *at birth* is higher in populations with better conditions, expected *adult* lifespan does not differ to the same degree; and ii) explains neither why women live significantly longer than men (Griffin et al. 2018) nor how it leads to reproductive cessation in long-lived women (Croft et al. 2015).

Among the adaptive hypotheses, the first of note is the 'mother hypothesis', sometimes also called the 'stopping early hypothesis'. The general gist of this hypothesis is that women stopped reproducing later in life to gain fitness from investing in children already born (Williams 1957), with assumed costs of continued reproduction from i) increased risk of maternal death, ii) increased risk of infant death, and iii) decreasing quality of offspring with age. Despite the probability of dying in childbirth increasing with age for mothers, this is likely of limited biological importance - the magnitude of increase has been shown to be low in pre-industrial populations, even when applying a hypothetical exponential increase from the age of actual reproductive cessation to age 70 (Lahdenperä et al. 2011a). Maternal death is widely known to be detrimental to infant survival (Sear & Mace 2008; Lahdenperä et al. 2011a), but the loss of a mother later in childhood often has negligible effects on short-term life history outcomes and more of an effect on long-term fitness (Sear & Mace 2008; Lahdenperä et al. 2011a). In killer whales, however, loss of a mother later in life is associated with a short-term decrease in survival probability of adult offspring, particularly sons (Foster et al. 2012), suggesting that the pathway to PRLS is not necessarily shared between the menopausal species. The final element of the mother hypothesis - decreasing quality of offspring with maternal age - cannot be explicitly tested in humans as reproduction does not continue until death, although the risks of miscarriage and chromosomal abnormalities are known to increase with age (Laisk et al. 2018), and these do negatively affect fitness. This should not be assumed to be an important evolutionary factor however – the elevated risks may be an inevitable consequence of reproductive senescence, and if women could continue to reproduce then these risks may only be higher at the end of the reproductive lifespan. Human PRLS, therefore, is highly unlikely to have derived from the (minimal) costs of continued reproduction.

Whether the decoupling of somatic and reproductive senescence was under selection or not in our evolutionary past (and in that of other animals with extended PRLS), is important and unknown. Currently, the most plausible hypothesis for selection for menopause directly (as opposed to selection only on lifespan after random mutations had already decoupled lifespan and reproductive lifespan) is the 'reproductive conflict hypothesis', proposed by Cant and Johnstone (2008). Reproductive overlap of generations and the potential for reproductive conflict between the overlapping generations is near-universal in animals (Cant & Johnstone 2008), yet humans are an exception to this. In situations where human dispersal is female-biased, co-living of mother-in-law and daughter-in-law occurs which creates a relatedness asymmetry within the patrilocal household. Both have a relatedness coefficient of 0.5 to their own child, the mother-in-law has an average coefficient of relatedness of 0.25 to the daughter-in-law's child, and the daughter-in-law is unrelated to the mother-in-law's child. Assuming costs of co-breeding to both the daughter-in-law's and mother-in-law's offspring, the evolutionary stable strategy is for the older female to commit to zero reproduction when the younger female reproduces (Cant & Johnstone 2008): the daughter-in-law is insensitive to the loss of the mother-in-law's child, whereas the mother-in-law loses indirect fitness if the daughter-in-law loses a child. Therefore, the fitness costs of co-breeding (no fitness) are greater than the fitness costs of not reproducing (loss of direct fitness – gain of indirect fitness = 0.25). In situations without relatedness asymmetries (i.e. unrelated reproductive women co-residing), reproductive conflict can be of detriment to the children (Pettay et al. 2016) but does not necessarily affect reproductive scheduling as there is no fitness (and therefore evolutionary) benefit to giving ground to 'rivals' (Pettay et al. 2018). Though it is more difficult to empirically test intergenerational reproductive conflict – menopause means there is little reproductive overlap – there is some supporting evidence for negative effects from both human and killer whale populations (Lahdenperä et al. 2012; Mace & Alvergne 2012; Croft et al. 2017). The reproductive conflict hypothesis remains a compelling one, and lack of negative overlap effects does not rule it out, particularly as this is an evolutionary conflict that – if true – has already been 'solved' by menopause and that the largest detrimental effects of overlap are evolutionarily constrained from occurring.

The third main adaptive hypothesis, and the one central to this thesis, is the 'grandmother hypothesis'. This posits that the indirect fitness benefits from helping to increase the reproductive fitness of offspring could select for longer life after menopause (Hawkes et al. 1998). There are two pathways to indirectly increasing fitness for grandmothers: increasing the number of grandchildren they have by aiding in the fertility of their offspring and increasing the number of grandchildren surviving to maturity. The lost direct fitness from ceasing reproduction (0.5 per possible child) would be counterbalanced by two grandchildren (0.25 per possible

grandchild) that would not have been born/survived childhood were it not for the grandmother. There is widespread empirical support for grandmother presence to accelerate reproduction (Sear & Coall 2011) and to increase child survival (Sear & Mace 2008), though, as with most work on humans, there is cultural and geographical variation in these outcomes.

Among the other menopausal species (see 1.1), evidence for beneficial life history outcomes of grandmother presence can be found in killer whales (Ward et al. 2009; Nattrass et al. 2019). Unfortunately, data on possible grandmothering behaviours in the other menopausal species are not available, and as such one cannot make any claims regarding grandmothering always being a component of extended post-reproductive life. Regardless, the presence of inclusive-fitness-boosting grandmothers in at least 2/5 of these species suggests that grandmothering may have played some role in facilitating the evolution of PRLS.

Grandmothers engaging in kin-directed behaviour is not a phenomena limited to menopausal species though, and can also be observed in other animals, such as African lions (*Panthera leo*) (Packer et al. 1998), Asian elephants (Lahdenperä et al. 2016), olive baboons (*Papio anubis*) (Packer et al. 1998), vervet monkeys (*Cercopithecus aethiops sabaeus*) (Fairbanks & McGuire 1986), Seychelles warblers (*Acrocephalus sechellensis*) (Richardson et al. 2007), and Japanese macaques (*Macaca fuscata*) (Pavelka et al. 2002). The nature of grandmothering in these non-menopausal species can differ quite substantially from that of humans and killer whales, to the point that their grandmothering is mutually exclusive with extended post-reproductive life. This is best illustrated with African lions, in which grandmother help is in the form of allolaction (providing milk), and the grandmother is unable to lactate without having her own infant cub (Packer et al. 1998).

From this, we can conclude that grandmothering will not always be a pathway/contributing factor to the evolution of PRLS and not enough for the evolution of menopause, but this does not prevent it from influencing selection on PRLS after somatic and reproductive senescence are decoupled, nor from influencing female lifespan in the absence of menopause. Indeed, recent comparative work has shown that mammalian species with grandparental care have a greater female bias in lifespan than other polygynous species (Péron et al. 2019).

Hereto, the benefits of grandmothers to grandchildren have often been considered in rather simplistic terms: present or absent from a population, and therefore supporting or not supporting the grandmother hypothesis. Uncovering the situations under which there are tangible benefits to fertility or survival from grandmother presence is crucial to furthering our understanding of just how important an evolutionary driver grandmothering could be.

1.3 Grandmothering contexts

1.3.1 Demography of grandmotherhood

In investigating cooperative behaviour, it is important to first understand the demographic situation - though the presence of helpers may produce beneficial outcomes, the evolutionary significance of helping behaviours may be reduced by unfavourable population demographics. Assessing demography allows us to quantify both the opportunity to help (e.g. helper availability) and the need for help (e.g. through quantifying childhood survival). Unlike other cooperative breeders, where help may be constrained by unfavourable environments (Emlen 1982) and helpers are pre-reproductive, human grandmothers do not seek to disperse to find mating success and are instead limited by longevity. The shared time of grandmothers and grandchildren – how long they live at the same time - is crucial for setting the stage for cooperative behaviour (Chapman et al. 2017) and gives a population-level measure of the opportunity for help. As such, chapter **I** focuses on these grandmother-grandchild demographics, with a particular focus on the opportunity for help to occur.

1.3.2 Grandmother lineage

Grandmother lineage is perhaps the most studied context of grandmothering, thanks in no small part to researchers in the social sciences – grandparental investment and health outcomes thereof to both grandchildren and grandparents are of rising importance as population demographics in industrialised countries become increasingly skewed towards older generations. From a more evolutionary perspective, there can sometimes be a fertility benefit to having either the (grand)mother or mother-in-law (paternal grandmother) present (Tymicki 2004; Lahdenperä et al. 2004; Sear & Coall 2011), though studies do not always distinguish between lineages or between grandparent sets (e.g. models may compare maternal and paternal grandparents, and not the grandmothers specifically). Paternal grandmothers, rather than improving grandchild survival, may improve the fertility of their children (the middle generation) in some populations (Sear et al. 2003; Tymicki 2004; Mace & Sear 2005; Tanskanen et al. 2014), but this is by no means universal.

Indeed, when all grandchild outcomes are considered, it is maternal grandmothers who are often seen to be more beneficial, such as for growth and nutrition (Hawkes et al. 1997; Sear et al. 2000; Sheppard & Sear 2016), mental health and cognitive development (e.g. Tanskanen & Danielsbacka 2012), and, of direct evolutionary importance, survival (Sear et al. 2002; Jamison et al 2002; Ragsdale

2004; Beise 2005; Leonetti et al. 2005; Sheppard & Sear 2016). However, grandchildren do not always have increased survival from maternal grandmother presence (Kemkes-Grottenthaler 2005; Sear 2008), and it may even be detrimental to have a living grandmother (e.g. Strassmann 2011).

Paternity uncertainty (Figure 1) is perhaps the most commonly raised explanation for these differences in grandmother investment (Euler & Weitzel 1996; Chrastil et al. 2006; Coall & Hertwig 2010; Tanskanen et al. 2011). Only the maternal grandmother has any certainty of grandparentage and would be predicted to invest the most. However, social context is highly important (Coall & Hertwig 2010; Chapman et al. 2018) – for example, residence patterns - and for those populations in which paternity uncertainty is an unlikely driver of lineage differences (e.g. paternal grandmothers are more beneficial), we must consider alternative explanations. Chapter **II** investigates how both offspring fertility and grandchild survival are affected by maternal and paternal grandmothers, as well as discusses possible drivers of any differences.

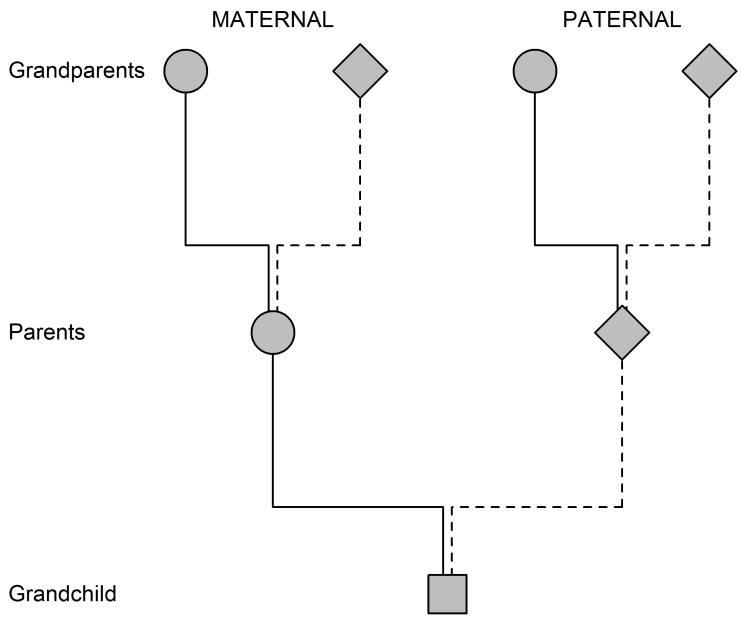

Figure 1. **Paternity uncertainty of grandmothers.** Women indicated by circles, males by diamonds. Solid lines indicate certainty of parentage, whilst dashed lines indicate uncertainty of parentage. The maternal grandmother has no uncertain links to her grandchild, whilst the paternal grandmother has one uncertain link, from her son to her grandchild.

1.3.3 Grandchild sex

One of the more recent hypotheses for differential investment into grandchildren by maternal and paternal grandmothers relates to differential inheritance of the X-chromosome: the X-linked Grandmother Hypothesis (Fox et al. 2010). The relatedness of the grandchildren can vary by sex, as grandsons only have a single X-chromosome, whilst granddaughters have two (Figure 2).

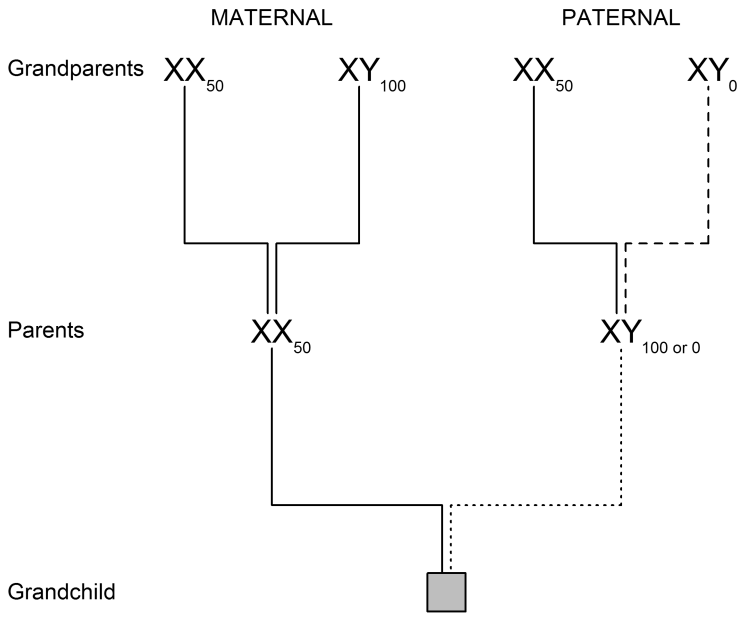

Figure 2. **Differential X-chromosome relatedness.** Women indicated by XX, men by XY. Numbers indicate the likelihood of any individual gene on the X-chromosome being passed to the subsequent generation. Solid lines indicate transmission of the X-chromosome, whilst dashed line indicates no transmission of the X-chromosome. The dotted line indicates variable transmission, based on the sex of the child - 100% X-chromosome relatedness if a daughter, 0% if a son.

For each X-chromosome gene, a grandmother has a 50% likelihood of passing it to her child. A mother then has a 50% chance of passing any particular X-chromosomal gene to her child (of either sex), leading to an average 25% relatedness (50% x 50%) of maternal grandmothers to granddaughters and to grandsons. A father has 100% chance of passing on X-chromosomal genes to a daughter and 0% to a son, leading to X-chromosomal relatedness of the paternal grandmother of 50% (50% x 100%) to granddaughters and 0% (50% x 0%) to grandsons. By ordering the relatedness via X-chromosome genes, we can get a continuum of grandmaternal care (ordered from highest to lowest):

paternal grandmother to granddaughter (50%)
>
maternal grandmother to granddaughter (25%)
=
maternal grandmother to grandson (25%)
>
paternal grandmother to grandson (0%)

Three testable predictions arise from this continuum: i) the favouring of granddaughters over grandsons by paternal grandmothers, ii) that maternal grandmothers are more beneficial for grandsons than paternal grandmothers, and iii) that paternal grandmothers are more beneficial for granddaughters than maternal grandmothers.

Up to this point, only the original study by Fox and colleagues (2010) had tested the X-linked Grandmother Hypothesis in relation to evolutionary important traits (i.e. survival). However, the predictions of the hypothesis do not appear to hold in contemporary populations when considering grandparental investment as a measure of (self-reported) contact time and quality (Tanskanen et al. 2011). Chapter **III** revisits the X-linked grandmother hypothesis to investigate whether it can indeed be considered as a vital component of grandmothering to consider in future studies.

1.3.4 Adverse birth status

The life history of individuals can be affected by many different familial contexts, including the circumstances of birth. A number of these 'birth statuses' have been shown to be detrimental to outcomes for children: i) firstborn children have a number of disadvantages (Juntunen et al. 1997; Wells et al. 2011), which may extend to decreased survival compared to non-firstborns (DaVanzo et al. 2008; Faurie et al. 2009; Mikshra et al. 2018); ii) birth spacing is also critical, with reduced survival for those born on either side of a short birth interval (under 24 months) (Rutstein 2005; DaVanzo et al. 2008; Molitoris 2017; Ahrens et al. 2018); iii) twins have an increased mortality risk relative to singleborns (Gabler & Voland 1994); and iv) children born to single mothers may be at greater risk of death in childhood (Sovio et al. 2012). However, work has yet to focus on whether grandmothers could possibly help in these situations.

Therefore, chapter **IV** focuses on whether grandmother presence can mitigate detrimental early-life survival effects for: i) firstborn children, ii) twins, iii) those born after a birth interval of less than 24 months, iv) those born before a birth interval of less than 24 months, and v) illegitimate children.

1.3.5 Grandmother age

Whilst the opportunity to help may depend heavily on the shared time between grandmothers and grandchildren (Chapman et al. 2017), it can also depend on when grandchildren are born during the grandmother's life, with grandchild births tending to be less common as women age (and therefore there are fewer opportunities to aid grandchildren later in life). Such a decline in opportunity would lead to a reduction in selection for continuation of life. The first element of chapter **V** is concerned with quantifying this side of helping opportunity.

This is not the only element of grandmother age that needs to be considered. Is there a decline in the ability to care? In many hunter-gatherer populations, post-reproductive women are typically net producers of calories (e.g. by digging up tubers) but their ability to provide declines and eventually they switch to being net consumers at a certain (population-varying) age (Hill & Hurtado 2009). Chapter **V**, therefore, also investigates whether helping effects are maintained across grandmothering ages, or whether they too decline.

1.4 Aims

To recap: i) despite the importance of context-dependent help in the cooperative breeding literature, this has not really been applied to humans; ii) extended post-reproductive lifespan is exceedingly rare, and we don't yet know what led to its evolution; iii) the indirect fitness benefits from grandmothering post-reproductively have been hypothesised to be a driver of extended PRLS iv) selection from contextually beneficial grandmothering will differ from continuously beneficial grandmothering, which may have implications for the role of grandmothering in the evolution of PRLS.

Therefore, the overall aim of this thesis is to quantify how the survival benefits grandmothers confer to grandchildren are affected by different contexts, and to discuss what consequences context-dependent help has on selection for post-reproductive longevity in humans. I will do this over five chapters, using an extensive multigenerational dataset on pre-industrial Finns.

Chapter I quantifies how the shared time between grandchildren and grandmothers - the major limiter for non-inherited effects of care and a prerequisite for any helpings effects to emerge and lead to the evolution of PRLS - changed across the demographic transition and with the progress of industrialisation, and suggests the role various key demographic traits may have played in these changes.

Chapter II investigates whether differences in grandchild survival exist between those individuals with living paternal or maternal grandmothers, whether such effects operate only at specific stages of childhood, whether maternal and paternal

grandmothers differentially affected the reproduction of their offspring, and what might be driving any (potential) differences.

Chapter III examines whether there is differential investment in the sexes by maternal and paternal grandmothers, and therefore also serves to test the predictions of the X-linked Grandmother Hypothesis in a pre-industrial, agrarian society: i) paternal grandmothers increase survival of granddaughters more than that of grandsons, ii) maternal grandmothers have a greater influence on survival of grandsons than paternal grandmothers, and iii) that paternal grandmothers have a greater influence on survival of granddaughters than maternal grandmothers.

Chapter IV explores whether a suite of birth statuses associated with reduced survival outcomes can have their detrimental effects lessened by grandmother presence: i) firstborn children; ii) twins; iii) children born following a short interval (less than 24 months); iv) children followed by a short birth interval; and v) illegitimate children.

Chapter V investigates how grandmother effects on grandchild survival change by grandmother age and health, and the potential for selection on post-reproductive longevity that this creates. Additionally, this chapter further quantifies the opportunity women had to post-reproductively help.

2 Methods

2.1 Study population

All chapters of this thesis use a long-term demographic dataset on humans from Finland. This dataset was derived from Lutheran church registers and, for more recent individuals, from published genealogies. Finland is one of the few countries in the world with comprehensive historic demographic data: from 1686, the Finnish clergy were legally required to collect information on their parishioners under the Swedish Church Law (Sweden ruled Finland until 1809), and by 1749 this was being done for the entire country (Gille 1949). The population was almost entirely Lutheran (following doctrinal reform of the church in the 1500s), and therefore these registers captured nearly every individual born in Finland. Information collected by the clergy included births/baptisms, deaths/burials (often including stillbirths and infants dying before baptism), marriages, children, occupations, location, and dates of communion (as well as other religious matters). The latter was important at the time for assessing the religious commitment of parishioners, and at present for establishing when a person was last known to be alive in the absence of a recorded date of death. Reason for death was also noted, though this was assessed by the recording clergymen and may not always accurately reflect the actual cause – "*isorokko*" (smallpox) is both a definitive cause of death and relatively simple to diagnose, whilst the much vaguer "*heikkous*" (weakness) reflects symptoms rather than cause.

Finland was a predominantly agrarian society in the time before industrialisation. Cultivation of arable land was the primary farming method across the country (Holopainen & Helama 2009), with eastern parts of Finland often using slash-and-burn on forested areas. The prevalence of this latter technique diminished over the 19th century (Moring 1999). Meat and fish were not a large part of a typical diet (around 10%, though fish would have been more commonly eaten in coastal areas), with the majority of energy consumption coming from rye (around 60%), barley (6-7%), and potatoes (9-12%) (Vihola 1994). Agricultural technologies and techniques were basic, with no wheel plough, poor drainage, and little fertilisation (Holopainen & Helama 2009), and localised famines were not uncommon. Countrywide famines were rarer, but devastating: more than a quarter of the entire population died during

the 1695-1697 famine (Lappalainen 2014), and there were high death tolls in the 1866-1868 famine (Pitkänen & Mielke 1993). Even in years of reasonable harvest, up to 10% of the population consumed nutritionally-poor substitutes, such as tree bark (Soininen 1974). As was typical for historic populations, birth rates and child mortality rates were high, and adult longevity was lower than in contemporary industrialised societies. Industrialisation in Finland began in the latter part of the 1800s (Hjerppe 1989), alongside the demographic transition, which began in the 1870s (Scranton et al. 2016). With industrialisation came advances in hygiene standards and medicine that would have had a role in decreasing childhood mortality and increasing longevity.

In the southwest, households were large for much of the 18th century, composed of either extended family groups, multiple co-residing (but related) families, or families with temporary servants. This was out of necessity, as farms required a labour force larger than the basic nuclear family unit. Patrilocal residency was common for the eldest son for reasons of inheritance, whilst younger siblings would temporarily reside in these larger households based on the labour requirements of the farm (Moring 1993). Many worked as farmhands or as maids for a time, though this does not appear to have been a permanent social position (Moring 1993). Nuclear households, however, became more dominant during the 19th century as restrictions on the division of land were loosened (Moring 1993). In the east, large households were also common, especially among farmers (Moring 1999). Inheritance in this area of Finland was related to household occupancy, and as such patrilocality was prevalent amongst landowning families (Moring 1999). Servants were much rarer in the east than they were in western Finland (Moring 1999), but most people were still involved with farming in some capacity during their life. As industrialisation progressed, households reduced in size as more children left to find work in industry e.g. in sawmills.

The study dataset contains nearly 100,000 individuals, born between 1535 and 2012 (though only 100 individuals pre-date the 18th century, and only 335 were born in the 21st century), spanning not only industrialisation and the first demographic transition, but also extended periods of Swedish and Russian rule, and eventual independence in 1917. Due to the detail in the registers, it is possible to trace back familial lineages - up to 15 generations in some cases. Extra-pair paternity is likely to have been low, so these lineages can be trusted even without genetic confirmation: the church forbade divorce outside of exceptional circumstances and the stigma of - and punishment for - adultery was great (Sundin 1992), and historic extra-pair paternity in Europe has been – on the basis of the Y-chromosome – to be much lower than previously thought (Larmuseau et al. 2016; Larmuseau et al. 2019). As register information is not openly accessible for the past 100 years for individuals who may still be alive, many individuals alive in the beginning of the 20th century were

censored (i.e. no recorded date of death) and some families could no longer be followed. Later information was therefore gathered from published genealogies (Liu & Lummaa 2014). From the basic demographic information available, it is possible to calculate a wide variety of traits relevant to life history, such as birth order and interbirth interval.

Individuals all lived in, or are from lineages originating in, eight 'study' parishes (Figure 3): the archipelago parishes of Hiittinen, Rymättylä, and Kustavi in Southwest Finland; Tyrvää and Ikaalinen in the Pirkanmaa region; Pulkkila, the northernmost parish, in Northern Ostrobothnia; and Jaakkima and Rautu, both in present day Russia after the Karelian Isthmus and Ladoga Karelia (together, Finnish Karelia) were ceded to the Soviet Union in 1940 and again in 1944 following the Winter and Continuation Wars (1939-1940; 1941-1944) respectively. In covering such a range of parishes, the dataset can be considered more representative of Finland as a whole (though study parish was still statistically controlled for, as described in the relevant chapters).

A large proportion of the study population worked as farmers, as "*talollinen*" (landowning farmer), "*mäkitupalainen*" (crofter), or "*torppari*" (tenant farmer). Others working on the farms were classed as "*renki*" (farmhand) or "*piika*" (maid). In the archipelago parishes of the southwest, people may have worked at sea as "*kalastaja*" (fisherman) or, increasingly during the 19th century, "*merimies*" (sailor). Craftsmen were moderately wealthy, with "*suutari*" (cobbler) and "*räätäli*" (tailor) among the most common. From these occupations, rough social classes can be constructed. Few were listed as "*sotilas*" (soldier), and those who were often also had another occupation, possibly indicative of conscription rather than a professional standing army. War was not, however, unknown to the Finnish populace during this time, with Sweden's conflicts with Russia - the Great Northern War (1700-1721), the Hats' War (1741-1743), and the Finnish War (1808-1809) - and Finland's position between the two nations leading to periods of Russian occupation: "*Isoviha*" ('Great Wrath') from 1713-1721, "*Pikkuviha*" ('Lesser Wrath') from 1742-1743, and incorporation into the Russian Empire as an autonomous Grand Duchy from 1809. As mentioned earlier, Finland and the Soviet Union fought against each other in the Winter War (1939-1940) and the Continuation War (1941-1944). Additionally, a requirement of the Moscow Armistice (which brought the Continuation War to an end) was that the Wehrmacht had to be expelled from Finland, leading to the seven-month Lapland War against Nazi Germany from late 1944 to mid-1945.

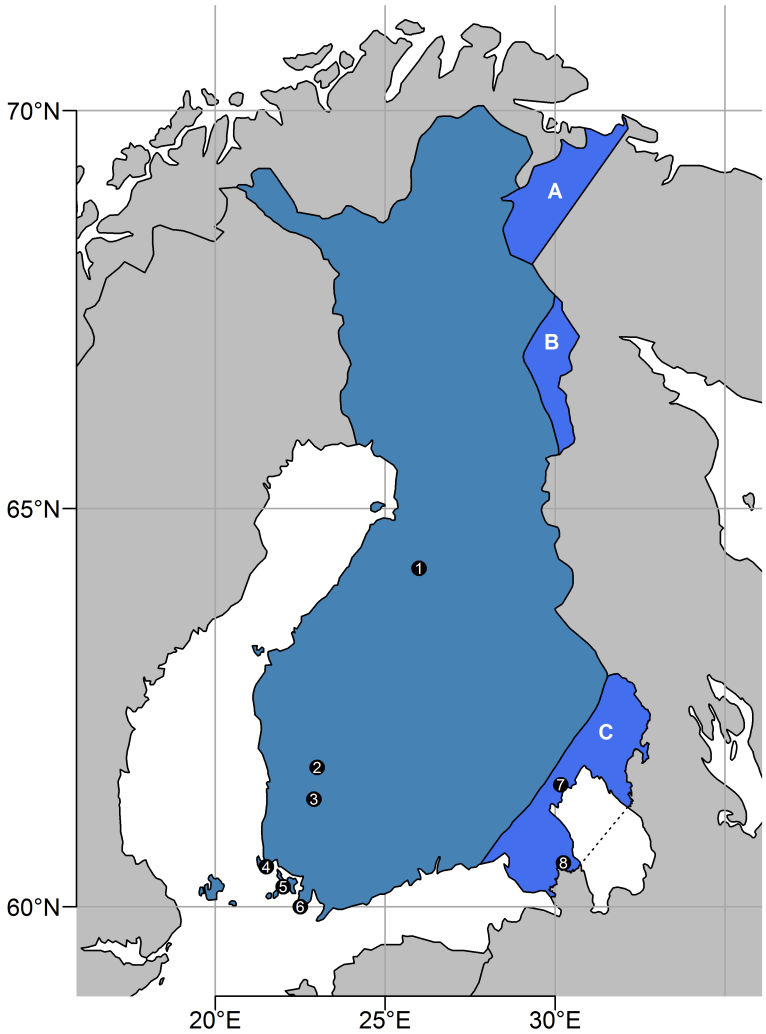

Figure 3. **Map of study parishes within Finland.** 1) Pulkkila, 2) Ikaalinen, 3) Tyrvää, 4) Kustavi, 5) Rymättylä, 6) Hiittinen, 7) Jaakkima, 8) Rautu. These parishes could all be considered rural. Filled brighter blue areas show the approximate size of regions ceded to the Soviet Union: A) Petsamo (which only became part of Finland in 1920), B) Salla-Kuusamo, and C) Finnish Karelia (comprising the Karelian Isthmus to the west of Lake Ladoga, and Ladoga Karelia to the north).

2.2 Data selection

All data selection and analyses in this thesis were conducted with R statistical software (64 bit), versions 3.3.1 (R Core Team 2016) (**I**, **III**), 3.5.1 (R Core Team 2018) (**II, V**), and 3.4.2 (R Core Team 2017) (**IV**). Data manipulation was predominantly done using base R operators and functions, but some additional packages were necessary. In chapter **I**, the *glance* function from R package *broom* (Robinson & Hayes 2018) was used to get the average values for each cohort from cox proportional hazard model outputs (see 2.3.1), and for the discrete time-event analyses (chapters **II**-**V**; see 2.3.2), I used the *unnest* function from R package *tidyr* (Wickham & Henry 2018) to expand the dataset from one row per individual to one row per year of life of each individual. Additional criteria for data selection can be found in the methods section of each chapter.

2.2.1 Study period

Though the records in this dataset come from as early as 1535, this thesis only covers a period of 1731-2016 (a breakdown of study period for each chapter can be found in Table 1), with the first focal individual (i.e. grandchild) born in 1731 (chapters **II**-**V**), and the last born in 1959 (chapter **I**). Whilst a longer timespan would be preferable, and particularly well-suited for investigating changing effects over time, conducting research on intergenerational relations necessitates that grandmothers and grandchildren are present in the dataset. The first grandchild with a known grandmother was born 1656, though there were fewer than 130 grandchildren in this dataset from before 1749, when comprehensive recording by Lutheran clergymen began. Relevant parent and grandmother information could be taken from some of those born in the 17th century, with the earliest individual used in this thesis born in 1674 in Tyrvää (grandmother to one grandchild).

Table 1. **Study periods, year of last birth of grandchild, and parishes used in each chapter.** Parish codes: HI - Hiittinen, IK - Ikaalinen, JA - Jaakkima, KU - Kustavi, PU - Pulkkila, RA - Rautu, RY - Rymättylä, TY – Tyrvää.

CHAPTER	PERIOD	LAST INDIVIDUAL BORN	PARISHES
I	1790-2016	1959	HI, IK, JA, KU, PU, RA, RY, TY
II	1731-1905	1890	HI, IK, JA, KU, PU, RA, RY, TY
III	1731-1885	1880	HI, IK, JA, KU, PU, RA, RY, TY
IV	1731-1895	1890	HI, IK, JA, KU, PU, RA, RY, TY
V	1731-1895	1890	HI, IK, JA, KU, PU, RA, RY, TY

Chapter **I** covered the most extensive period of time (170 years of births). Births of grandchildren were considered up to 1959, as after this point there was a much higher level of censoring, which would have given a highly inaccurate representation of demographic patterns in those later decades. Chapters **II**, **III**, **IV**, and **V** were mostly pre-industrial, though some births occurred in the late 19th century, after the onset of the demographic transition. However, the progress of industrialisation and the transition was slow (Scranton et al. 2016), and these later decades could therefore be considered as more similar to pre-industrial life than to a contemporary industrialised society.

2.2.2 Selection of time-event data

After data were transformed into a time-event format, allowing variables to differ between discrete units (here, years), I added the survival variable (or reproduction in one analysis in chapter **II** – see 2.3.2). Values were set to 1 in a year of not dying and 0 in the year of death. Following standard practice, the values for fertility analyses were coded as 1 in the year of reproduction and 0 in years of not reproducing. If there was no recorded date of death, the focal individual was censored at the last year of they were known to have been alive. For example, a three-year-old who died would be have the values of 1, 1, 0, and a censored three-year-old would have the values 1, 1, 1, and would not then be included in the dataset for the following year. Individuals were also censored in the year a grandmother (or mother/mother-in-law in the fertility analysis) disappeared from the records, and when individuals lived until age 15 (chapter **II**), age 5 (chapters **II**, **III**, **IV, V**), or age 2 (chapters **II**, **III**, **IV**, **V**), dependent on analysis.

In addition, I removed observation years in which a grandchild was censored at the same time as their mother, as this could indicate an event at the family-level, and individuals if they died within a week of their mother's own death, which suggests high dependency, and would therefore be unpreventable by grandmother intervention. See 2.3.2 for analytical details.

2.2.3 Age of grandchildren

I defined childhood as anything up to an individual's 16th birthday (following Lahdenperä et al. 2004). When appropriate for analysis, I divided childhood into three stages: infancy (0-2), toddler (2-5), and late childhood (5-15), with age ranges inclusive of the left border, and exclusive of the right (except for 5-15, which included the 15th year of life as well). Infancy encompasses the period when a child is still at the mother's breast, which may have reduced the influence of grandmothers if help was via extra provisioning, for example. The toddler stage could be

considered the most critical for survival that could be affected by grandmothers - children are weaned but are still highly dependent on others. Children are more independent after this point, and survival rates are much higher. Childhood mortality of individuals used in this thesis was nearly 33%, with just over ¾ of these deaths occurring before a child reached their 5th birthday.

2.3 Statistical analyses

Model specifics, additional variables, and other statistical information not detailed here can be found in the methods section of each chapter. Statistical significance in this thesis is defined at the level of $\alpha = 0.05$.

2.3.1 Time-trend analyses

I implemented cox proportional hazards models with the *Surv*, *survfit*, and *coxph* functions from the *survival* R package (Therneau 2015) in **I**, to obtain predictions of the length of time grandchildren-grandmother dyads would last across seventeen 10-year birth cohorts, and for average grandmother age at grandchild birth and average number of grandchildren. Cox models were used to account for censored lifespans; the cohort averages would be biased downwards were censored cases to be treated as deaths, and this would have particularly affected the 20th century cohorts. To calculate the per-cohort values for the percentage of grandchildren a) having a grandmother alive at birth, outliving a grandmother, and c) living in the same parish as a grandmother, I simply divided the number of grandchildren meeting the criterion of interest by the total number in that birth cohort, then multiplied by 100. Spearman's rank correlation coefficients were calculated to indicate whether significant change had indeed occurred over time. Only the grandmother-grandchild relationship was assessed in this chapter, as grandfathers did not have any great presence in the lives of their grandchildren (Chapman et al. 2017), and they had no impact on grandchild survival in this population (Lahdenperä et al. 2007).

2.3.2 Discrete time-event analyses

In chapters **II-V**, I used generalised linear mixed-effects models (GLMMs) using the *glmer* function from the *lme4* R package (Bates et al. 2015) to assess differences in grandchild survival by a) maternal and paternal grandmother presence (i.e. lineage differences; **II** & **III**), b) the sexes of grandchildren (**III**), c) grandchild age (**II**, **III**, **V**), d) adverse birth statuses (**IV**), and e) grandmother age (**V**), and also to assess differences in fertility by mother or mother-in-law presence (**II**). All GLMMs were binomial time-event models, with the response variable set as child survived that

year or died, or woman reproduced in that year or did not (for the fertility analysis in **II**). I used the *nloptwrap* optimiser instead of the default optimiser for *lme4* to reduce computation times - results were not affected by the choice of optimiser.

2.3.2.1 Model selection

For each study, a full model was constructed with all possible confounding variables. I then sequentially removed terms, comparing the Akaike Information Criterion (AIC) value of the full model to each model with a removed term. If the AIC increased by >2 compared to that of the full model, that term was retained for the proper analysis. Those decreasing the AIC were omitted, and if AIC was within 2 of the full model AIC, the most parsimonious model was used (i.e. the term was omitted). Random effects were not subject to this model comparison and were always retained. Odds ratios were calculated by exponentiation of model estimates, and confidence intervals for these odds ratios were calculated by taking the exponential of the estimate ± 1.95 times the standard error.

Table 2 describes the variables used in the GLMMs. It should be noted that focal individual identifier (ID) was not included as either a fixed or random effect, as within-subject correlations are not present in discrete time-event data: each year of life was considered as a separate observation (Allison 1982; Nitsch et al. 2014).

Table 2. **Variables used in final GLMMs.** Information on variables not included in any analysis after AIC-based model reduction can be found in the chapters. Time-varying variables are indicated by a *.

VARIABLE	TYPE	DESCRIPTION	CHAPTER
SURVIVAL OF GRANDCHILD*	Response	Binary: dead or alive	II, III, IV, V
REPRODUCTION OF WOMAN*	Response	Binary: reproduced or didn't	II
GRANDCHILD AGE*	Fixed	Age in years of focal individual	II, III, IV, V
WOMAN AGE*	Fixed	Age in years of focal individual	II
GRANDMOTHER TYPE*	Fixed	4-level factor: only maternal alive, only paternal alive, both dead, both alive	II, III, IV
MOTHER TYPE*	Fixed	4-level factor: only mother alive, only mother-in-law alive, both dead, both alive	II
GRANDMOTHER AGE*[A]	Fixed	4-level factor: dead, under 50, 50 to 75, over 75; continuous	V
GRANDMOTHER TIME TO DEATH*[A]	Fixed	4-level factor: dead, one year, two years, three plus years	V
TIME SINCE LAST BIRTH*	Fixed	Continuous	II

VARIABLE	TYPE	DESCRIPTION	CHAPTER
STATUS OF OTHER GRANDMOTHER*[B]	Fixed	3-level factor: alive, dead, censored	V
MATERNAL SURVIVAL STATUS*	Fixed	3-level factor: alive, dead, censored	II, III, IV, V
MATERNAL AGE AT BIRTH	Fixed	Continuous; linear & quadratic	IV
NO. LIVING SIBLINGS*	Fixed	Continuous	II, IV
NO. LIVING SIBLINGS AND COUSINS*	Fixed	Continuous	V
CHILDHOOD SOCIAL CLASS	Fixed	2-level factor: landed, landless	II, III, IV, V
GRANDCHILD SEX	Fixed	2-level factor: female, male	II, III, IV
BIRTH ORDER	Fixed	Continuous	II, IV
TWINNING STATUS	Fixed	2-level factor: not a twin, twin	II, III, IV, V
PARISH AREA[C]	Fixed	4-level factor: Southwest Finland, Pirkanmaa, Northern Ostrobothnia, Finnish Karelia	II, V
PARISH AREA[C]	Fixed	2-level factor: archipelago, mainland	IV
STUDY PARISH[C]	Random	8-level factor	III
GRANDMOTHER ID[D]	Random		II, III, IV, V
PARENT ID[D,E]	Random		II, III, IV, V
BIRTH COHORT[F]	Random	Varied by study period	II, III, IV, V

[A] Either maternal or paternal grandmother, but not both in the same model
[B] Paired with grandmother age; opposite lineage
[C] See 2.1 Study population for details. Parish area and study parish were never used in the same models
[D] Typically maternal grandmother and mother ID, though it does not matter if paternal grandmother and father: it makes no difference to results. As long as one parent and one grandmother ID is included to account for genetic similarities between siblings and cousins, it does not matter which parent/grandmother ID is used
[E] Nested in grandmother ID, except in fertility analysis of **II**
[F] 10-year bins

In the fertility analyses of **II** and in one analysis of **III**, I included interactions to establish whether there were interactive effects of variables on fertility and survival. Due to the way in which *lme4* outputs model estimates, significance of interaction terms as a whole cannot be immediately assessed. I therefore re-ran these models with the *mixed* function from R package *afex* (Singmann et al. 2017) to calculate a p-value for interaction terms via likelihood ratio testing. Though parametric bootstrapping would return more accurate values, it is also computationally unfeasible.

Grandmother age was assessed in two ways in **V**: as categorical and as continuous predictors. Whilst it is preferable for age to be considered in a continuous manner, continuous age can only indicate the effect of the presence of a grandmother of a certain age relative to other grandmother ages, and not against the essential baseline point of comparison of no grandmother. This cannot be incorporated into a continuous predictor, and therefore, it was not possible to investigate age effects on grandchild survival in this manner. The categorical predictor was divided on biological lines: age 50 is the upper age at menopause, and women younger than this may theoretically be physiologically capable of further reproduction (and introduce possible competition for their grandchildren); age 75 is around the lifespan of non-industrialised, traditional societies, which typically range from age 70 to 80 (Gurven & Kaplan 2007).

In **V** I also investigated child survival with grandmother time (in years) until death as the main predictor. In the absence of actual health records, this acts as a proxy of health: a grandmother living on for a number of years could be assumed to be in better condition than one dying the next year, particularly with the quality of medical care pre-industrially. As with grandmother age, this variable needed a baseline, and was therefore treated as categorical, with four levels to the factor: dead, 1 year to death, 2 years, and 3+ years. For further details, please refer to the methods section of **V**.

2.3.3 Hazard of death

In **V**, I determined Kaplan-Meier hazard estimates in order to obtain the age-specific hazard of death for women (following Lahdenperä et al. 2004). This was done with the *kphaz.fit* function from R package *muhaz* (Hess & Gentleman 2014).

2.4 Visualisation

The map (Figure 3) was produced with the *map* function from R package *maps* (Becker et al. 2018). Borders of the regions ceded to the Soviet Union were approximated from historical maps as the actual coordinates for these areas could not be sourced. Therefore, they should not be considered as 100% accurate, only illustrative of the general size and location of these lost territories.

All other figures in this thesis were produced with base R graphics and are intended to be colour-blind friendly.

3 Results & Discussion

3.1 Demography of grandmotherhood

Understanding the demography in which cooperation is being investigated is an important starting point, allowing us to establish the opportunity for help (e.g. time helpers are present) and the need for help (e.g. high childhood mortality). The nature of the grandmother hypothesis requires there to be benefits of the grandmother living, and I therefore first quantified the 'shared time' of grandmother-grandchild dyads - in other words, how long a grandchild and a grandmother would live at the same time on average. As such, I provide the demographic basis of grandmothering in this pre-industrial Finnish population in **I**.

I was able to show that the average shared time with maternal grandmothers was slightly higher than with paternal grandmothers and remained under 10 years in the pre-industrial period. Finland underwent a demographic transition in the mid-1870s (Scranton et al. 2016), after which one might expect the demographics of grandmotherhood to change in response to declines in fertility and childhood mortality rates. Indeed, shared time increased markedly for each subsequent birth cohort following the demographic transition, reach a high of ~20 years for the last study cohort (born in the 1950s). The opportunity for help therefore increased, though with the declining mortality and fertility rates that characterise the demographic transition, the need for life-history-affecting help is likely to have diminished. This is the typical scenario in industrialised societies (Uhlenberg 2004; Leopold & Skopek 2015a; Leopold & Skopek 2015b; Margolis 2016; Margolis & Wright 2017), with the role of grandmothers shifting towards improving sociological outcomes (Bengston 2001; Tanskanen & Danielsbacka 2018).

With the stage clearly set – grandmothers were typically present during the early childhood of their grandchildren – we move on to specific contexts.

3.2 Grandmother lineage & grandchild age

In chapter **II**, I found that not all grandmothers are equal: maternal grandmothers were more associated with positive outcomes to the evolutionary important fertility of offspring and survival of grandoffspring. Though there were no significant

grandmother effects on the age at first birth, I found that maternal grandmother presence, but not paternal grandmother presence (i.e. the mother-in-law), was associated with shorter birth intervals than if neither were present. These fertility effects depended somewhat on the birth order of grandoffspring and the age of the focal daughter, with shortest birth intervals for early birth orders and for younger focal daughters. This suggests that the presence of the grandmother during the reproductive lifespan of her daughter would lead to more grandchildren, and therefore supports one of the key elements of the grandmother hypothesis.

When investigating the effects of grandmother presence on grandchild survival outcomes, I found maternal grandmothers were associated with an increase in survival for toddlers (ages 2-5), but there were no effects for the rest of childhood. Paternal grandmother presence was not associated with survival effects in either direction.

Grandchild age is clearly a vital factor into whether a grandmother may or may not be helpful. Throughout the thesis I consistently found grandchild age to be important for survival outcomes (**II** & **V** in particular). Absence of early life survival effects is likely due to the inability of the grandmother to directly help – the child is mostly fed on the mother's breast milk, which cannot be supplemented by the grandmother. The beneficial survival effects come in the years post-weaning, when the child is no longer dependent on milk but is unable to independently sustain themselves.

Taken as a whole, this chapter shows that both elements of the grandmother hypothesis – positive effects on offspring fertility and grandoffspring survival – can be occurring at the same time. Whilst paternal grandmothers do not provide these same beneficial fitness outcomes, the contribution of the maternal side may be enough for positive selection on lifespan from the indirect fitness benefits.

In **II**, I also discuss why paternity uncertainty should not be used as a catch-all mechanism for lineage differences. Considering paternity uncertainty as the only driver of differences tends to ignore social contexts (Friedman et al 2008; Coall & Hertwig 2010; Kaptijn et al. 2013) and cannot be explicitly tested in historical societies without genotyping the dead - a whole new ethical minefield in and of itself. Lineage differences in pre-industrial Finland are, on the basis of historical societal contexts, highly unlikely to be driven by paternity uncertainty: monogamy was the enforced norm, with divorce forbidden by the church, and harsh punishments for adulterers (Sundin 1992). Additionally, extra-pair paternity rates in historical Europe have, on the basis of Y-chromosome inheritance, been estimated as very low (Larmuseau et al. 2016; Larmuseau et al. 2019).

If not paternity uncertainty, then what? One testable hypothesis for the lineage differences in grandmother effects is the X-linked Grandmother Hypothesis (Fox et al. 2010), which proposes that grandparental help will differ based on X-

chromosome relatedness. In **III**, I tested whether this pre-industrial Finnish population followed the predictions of this hypothesis, and in doing so discover whether this is a possible genetic mechanism for lineage differences.

3.3 Grandchild sex

The crux of the X-linked Grandmother Hypothesis is that the relatedness of grandmothers to grandchildren differs by a couple of percent due to the relative contribution of the X-chromosome to total genetic material (Fox et al. 2010). Paternal grandmothers are more related to their granddaughters on the X-chromosome than maternal grandmothers are, and also have the lowest X-chromosome relatedness to grandsons. Therefore, investment should be greatest from paternal grandmothers to granddaughters and lowest from them to grandsons. That grandsons are predicted to do slightly worse is to be expected, even without accounting for differential X-chromosome relatedness: raising males is more costly (Lummaa 2001).

In **III**, I found support for two of the three predictions of the X-linked Grandmother Hypothesis: paternal grandmother presence was better for the survival of granddaughters than grandsons, but worse for grandson survival compared to when the maternal grandmother was present. However, there was no statistically significant difference in granddaughter survival with the presence of paternal or maternal grandmothers, and therefore prediction iii remained unsupported. Whilst this may seem to contradict the findings of **II** (in that there is no lineage difference here), this analysis was attempting to replicate the findings of Fox et al. (2010), and the modelling structure used for this purpose does not permit direct comparison between analyses in **II** and **III**.

All three predictions must be supported for the X-linked Grandmother Hypothesis to be plausible in this population. The results of chapter III show this not to be the case. Without direct support - including from the original meta-analysis of Fox et al. (2010) itself (see discussion of **III**) - the hypothesis cannot be used as a general explanation for the lineage differences in grandmother effects (at least, not as the sole mechanism). Indeed, for the continuum to be of relevance, it would also require some innate recognition of these differences in relatedness to grandchildren - in a time largely predating knowledge of even the most basic form of genetic inheritance mechanisms. Furthermore, the hypothesis strips grandmothering of vital social contexts that may be far more important than minute variations in relatedness, such as whether wealth inheritance is patrilineal or not, or on the importance of the family name being passed on.

3.4 Adverse birth statuses

Contrary to initial predictions, grandmother presence did not improve survival for most of the adverse birth statuses examined in **IV**. Only those children born preceding a birth interval of 24 months or lower showed a higher probability of surviving to age five in the presence of a maternal grandmother.

As the beneficial effects of grandmother presence in this population are observed for grandchildren post-weaning (**II** & **V**), the lack of effects here may be because the negative effects on survival are only manifested in infancy (e.g. Bellizzi et al. 2018), before grandmothers are able to provide survival-affecting care. Those born preceding a short interval, meanwhile, must have survived at least until the birth of their younger sibling and are likely to be weaned.

One must be careful, however, in interpretation here. Might we find this beneficial effect because mothers are accelerating their reproduction in the presence of the maternal grandmother (e.g. **II**; Hawkes et al. 1997)? The outcome is of course the same - these children survive better than if the maternal grandmother was not present.

3.5 Selection on post-reproductive longevity from grandmothering

For grandmothers to be beneficial to grandchild survival, and for selection to operate, there must be both opportunity to help and need for help. The need element should, I hope, be clear at this stage – childhood mortality was high, particularly in early childhood. Opportunity, meanwhile, was partly quantified in **I**, though this does not provide the entire picture. In **V**, I show from age-specific birth rates of grandmothers (i.e. the rate at which grandchildren are born) that the opportunity to gain indirect fitness from the birth of grandchildren follows more-or-less the pattern of age-specific birth rates of mothers (Figure 1 of **V**). As one would logically expect, grandchildren are not born forever, and the opportunity to help therefore declines. However, as can be seen in the figure, there is still a sizeable chunk of (potential) indirect fitness gains that come after the typical adult lifespan of women of this population and other non-industrial societies (Gurven & Kaplan 2007). Concurrent with this, I found the hazard of death – an indicator of population senescence rates and of the weakening force of selection (Maklakov & Immler 2016) – to accelerate from the age of menopause. This acceleration was greater later in life – as written in **V**, the hazard of death at age 70 was three times greater than that at age 50, and at 80 it was six times greater. In practice, what does this mean? The opportunity and the need for grandmothers to provide care declined with age, and as such the force of selection on lifespan from grandmothering may be diminished.

The second part of **V** was concerned with the survival effects of grandmother presence by age. I found that maternal grandmothers were beneficial most of the time, but their presence did not increase grandchild survival if they were in the 'old' category. However, having a living but old paternal grandmother around lowered the probability of survival through infancy. It is better, then, for lifespan to be limited, with grandmothering unable to favour post-reproductive longevity indefinitely.

Why might we find a negative effect? As discussed in **V**, paternal grandmothers were typically the co-resident lineage, and this introduces several possibilities: i) they may stress their daughter-in-law during pregnancy (Beise & Voland 2002); or ii) declining health with age leads to an inability to provide and an increase in their own need for assistance, resulting in competition between grandmother and grandchild for parental resources. Whilst the former is unfortunately untestable with historic data, we were able to assess the effects of declining health. With grandmother health proxied as their time to death – with the very limited healthcare of the pre-industrial period, those in poor health were not likely to survive long - I showed similar results to those of grandmother age: maternal grandmothers further from death were beneficial, and those close to death were not. Paternal grandmothers were never beneficial, and those a year from death were associated with a reduction in survival.

3.6 Summary of main findings

Chapter I: the shared time of maternal grandmothers was around two years longer than paternal grandmothers; the demographics of grandmotherhood were relatively stable pre-demographic transition; following industrialisation and the demographic transition, the opportunity for grandmothers to help increased.

Chapter II: age at first birth was not earlier in the presence of either maternal or paternal grandmothers; maternal grandmother presence reduced inter-birth intervals; maternal grandmother presence only increased survival of toddlers (ages 2-5); there were no positive or negative survival effects of paternal grandmother presence for any age grandchild.

Chapter III: paternal grandmother presence was more beneficial to granddaughter survival than grandson survival; survival of grandsons was lowest when the paternal grandmother was present; paternal grandmother presence was not more beneficial for granddaughter survival than that of maternal grandmothers.

Chapter IV: there were no survival benefits to having grandmothers for most adverse birth statuses; maternal grandmother presence was beneficial for survival of children with a subsequent short birth interval, allowing faster reproductive rates for mothers

Chapter V: maternal grandmother presence was beneficial to grandchild survival only if the grandmother was in the age class 50-75 or was 2+ years from death; paternal grandmother presence was detrimental to grandchild survival if they were in the 75+ age class or within a year of death.

4 Conclusions

In this thesis, I aimed to discover whether life history outcomes of grandmother presence vary according to different contexts, and what effect this may have had on selection for extended post-reproductive lifespan. By taking inspiration from work on other cooperative breeders, I hoped to bring greater insight into the evolutionary benefit of grandmothers.

Perhaps the most important result of this thesis is from chapter **V**: fitness benefits of grandmothering can exert balancing selection on longevity, with positive selection on lifespan earlier on from beneficial effects and then selection against increased lifespan when grandmothers begin to negatively affect their own indirect fitness. As many non-industrial populations have similar lifespans (Gurven & Kaplan 2007; Hill & Hurtado 2009), replication of the study with other populations is vital.

I have also identified notable lineage differences in the survival outcomes of grandmother help, consistent with the general matrilineal bias found in other human societies. In chapter **II**, I discussed that the oft-cited, empirically unsupported concept of paternity uncertainty was unlikely to have driven these differences in the pre-industrial Finnish population on the basis of historical social contexts. In chapter **III**, I showed that slight differences deriving from X-chromosome relatedness similarly do not explain the differences in this population.

It is quite clear then, from an evolutionary perspective, that grandmothering does not provide a constant benefit to grandchildren. The survival of grandchildren is mediated by more than grandmother presence alone, and contextual information is key in determining when indirect fitness benefits of extended post-reproductive life arise. Given the vast body of research showing the context-dependence of helping outcomes in other cooperative breeders, this is not a particularly controversial claim, but is rarely addressed in human behavioural ecology. Grandmothering is unlikely to be a sole driver of menopause and extended post-reproductive lifespan, even if it were to be beneficial independently of environmental and social contexts.

This thesis was not undertaken with the aim of dismissing the grandmother hypothesis, but nor did I seek to elevate it above all else. Indeed, my findings place grandmothering firmly in the middle ground: grandmothers are beneficial in many situations, but equally context is crucial, and grandmothering cannot account for the

existence of extended human post-reproductive life alone (unless, of course, the strength of selection on grandmothering was much higher in the Pleistocene environment). The search for the missing pieces of the PRLS puzzle goes on.

4.1 Future directions

Finding that grandmothering does indeed vary under different contexts opens up plenty of new and exciting empirical and theoretical avenues of research. In this final section, I highlight some of these, both (relatively simple) short-term studies and more substantial directions the field could take.

4.1.1 Replication

From the literature, it is clear that the outcomes of grandmothering can differ greatly between populations. Future empirical research must, therefore, focus first on replicating the approaches of this thesis in other populations as the absolute minimum. Going further forward, as other contexts of possible significance are tested, they need replication. Only then will we begin to be able to piece together which contexts are truly important and which are population-specific and of negligible evolutionary significance. One such replication could be done already with this Finnish dataset – investigating how grandmother-associated survival outcomes are affected by distance, following work on register data from 17th-18th century Québec by Engelhardt and colleagues (2019).

4.1.2 Death in the family

Though each chapter of this thesis focused on specific contexts, there was one covariate that was of great importance: the survival status of the mother (i.e. the intermediate generation). In all chapters with survival analysis, the probability of grandchild survival was always significantly lower when the mother was recorded as dead versus alive. This shows a potential avenue of research in relation to human family-living (not just grandmothering) – when the primary caregiver dies, can kin step up and mitigate the detrimental effects? Caregiver death could be considered another context not explored in this thesis under which grandmothers could play an important role, and such losses were likely relatively common in the past, highlighting the importance of studying family composition in a dynamic manner.

4.1.3 Grandmothering over the demographic transition

In chapter **I**, I established that the demographics of grandmothering – particularly the opportunity to help – drastically changed. The story does not end there though. We know already that survival through childhood does not rely on grandmother intervention any longer, thanks to modern medicines and the sweeping societal changes of the last 100+ years. What we are yet to determine, however, is when the grandmothering benefit switched from the evolutionarily-important survival to improving equally important sociological and developmental outcomes, or favouring fertility outcomes. This particular direction has an interesting interdisciplinary aspect, bringing together evolutionary biology, history, and sociology to map the changing nature of the grandmother-grandchild relationship through time. The dataset used in this thesis is one of few in the world giving us an opportunity to investigate this too, and the access of sociologists to more recent population registers in Finland provides the prospect of a detailed timeline of how industrialisation and the demographic transition affects selective pressures on such traits as grandmothering.

4.1.4 Other contexts

My work here has only begun to scratch the surface of the different contexts under which grandmothering benefits might be manifested. In pre-industrial Finland, at least, grandmothering was certainly context-dependent, varying by: i) grandchild age; ii) grandmother lineage; iii) grandmother age; iv) grandmother health (proxied); v) grandchild sex (to a lesser extent), vi) birth status. All of these could be considered as intrinsic contexts, independent from the environment, leaving much scope for future work.

Both biological and societal contexts should be considered to get as complete a picture of the benefits of grandmothering as possible. One such biological example would be disease prevalence and whether grandmothers could mitigate the impacts of diseases. This could focus on e.g. childhood infectious diseases (so grandmothers would not be unwitting vectors). Again, Finland has exceptional records in this regard for the pre-industrial 18th and 19th centuries. A more societal context, but still biologically relevant, would be the outcomes of co-residence with grandmothers. In this population, we already know that co-residence between reproductive individuals can be costly (Lahdenperä et al. 2012; Pettay et al. 2016; Pettay et al. 2018), and I would like to investigate whether co-residence between pre-reproductive and post-reproductive individuals also leads to competition and detrimental outcomes on life-history.

4.1.5 Context-dependent grandfathering

One might quite reasonably ask whether grandfathers exhibit context-dependence too. Whilst grandfathers have no overall impact on grandchild survival in this pre-industrial population (Lahdenperä et al. 2007), nor any significant presence in the lives of their grandchildren at the population level (Chapman et al. 2017), it would be remiss of me to disregard them in their entirety. Do we find no effects because our view has been too broad?

Previous work in this population showed that men had shorter adult lifespans than women (Griffin et al. 2018), a pattern seen widely in contemporary human societies (Colchero et al. 2016), and this is reflected in age-specific hazard of death for pre-industrial Finnish men (Figure 4).

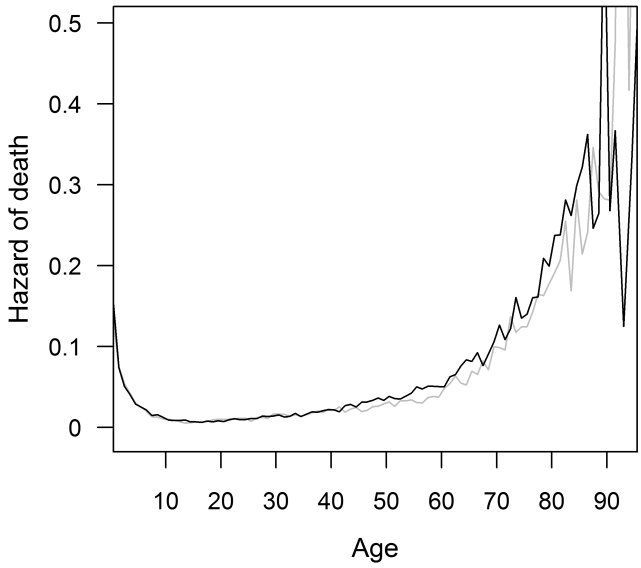

Figure 4. **Hazard of death in pre-industrial Finland.** The black line represents the hazard of death of men, whilst the grey line denotes the hazard of death of women (taken from chapter **V**). Acceleration in male hazard of death begins earlier than that of women, suggesting that male longevity could be under weaker (and likely different) selective pressures.

Acceleration in mortality - an increasing hazard of death - indicates increasing rates of senescence (Maklakov & Immler 2016), and the onset of this increase in men is years before that of women; we can infer there is stronger selection on female longevity than that of males. In monogamous populations, male longevity may even be selected against (Lahdenperä et al. 2011b), and remarriage of widowed men does not bring about increases in long-term fitness either (Pettay et al. 2014). With a

shorter 'opportunity' to help compared to grandmothers, and with seemingly different selective pressures on male longevity, it would be highly interesting to investigate whether grandfathers do become helpers under certain conditions.

4.1.6 Lineage differences

Whilst it is appealing to identify universal mechanisms of widespread patterns, my work here (**II** and **III**) and that of many others have shown that there is no consistent statistical support for any that have been proposed. One could take the conclusion here to be that the main driver is yet to be found, though the answer may simply - and perhaps unsatisfyingly - be that social customs combine together to drive differences. In other words, lineage differences are not innately biological, though they remain of huge biological importance.

This does not, however, prevent attempts to find a possible commonality in all the populations. Culture is clearly important, and by undertaking the difficult task of accounting for a whole suite of major cultural differences (e.g. dispersal patterns, marriage customs, expectations surrounding fertility and childcare), we might yet be able to uncover the underlying pathways to differences in maternal and paternal grandmothering benefits.

4.1.7 Modelling PRLS evolution

Whilst empirical studies can show us whether grandmothering is expressed or not, we must rely on theoretical models to see how context-dependence of grandmothering might have affected the evolution of PRLS. Such modelling can be used to show that grandmothering enables a transition from great ape-like longevities to higher longevities (Chan et al. 2016), that shortening post-reproductive lifespan reduces fertility of offspring and survival of grandoffspring (Aimé et al. 2017), and that conditions favouring emergence of menopause are different from those favouring maintenance of menopause (Thouzeau & Raymond 2017). By incorporating constraints into theoretical grandmothering models, we can shed light on whether investigated contexts are meaningful for human life history evolution. As a simple example, if we limit beneficial effects of grandmothers to only improve survival for children aged 2-5, can PRLS still arise and be maintained on an evolutionary timescale? How does this affect inclusive fitness? The potential here is vast.

4.1.8 A wider synthesis

Empirical tests of the role of culture in whether grandmother presence is beneficial or not are incredibly challenging to design. Even accounting for dispersal and co-residence patterns in relation to life history outcomes is difficult, in part due to lack of suitable data, and there will be many other elements of culture that cannot adequately be accounted for. Without cultural knowledge, the difficulty in determining the role of grandmothering in the evolution of extended post-reproductive lifespan is significantly ramped up, especially as we delve further back into the evolutionary past of humanity. Integrative multidisciplinary approaches from both empirical and theoretical perspectives may be the only way forward. Such a synthesis of often-disparate fields holds the potential to produce highly exciting and unorthodox hypotheses and results, even if the path ahead is difficult. I, for one, eagerly await to see how grandmothering research progresses.

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